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Social Learning Strategies: Bridge-building between fields

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Abstract: While social learning is widespread, indiscriminate copying of others is rarely beneficial. Theory suggests individuals should be selective in what, when and whom they copy, by following "social learning strategies" (SLSs). The SLS concept has stimulated extensive experimental work, integrated theory and empirical findings, and created impetus to the social learning and cultural evolution fields. However, the SLS concept needs updating to accommodate recent findings that individuals switch between strategies flexibly, that multiple strategies are deployed simultaneously, and that there is no one-to-one correspondence between psychological heuristics deployed and resulting population-level patterns. The field would also benefit from simultaneous study of mechanism and function.

SLSs provide a useful vehicle for bridge-building between cognitive psychology, neuroscience and evolutionary biology.

Social Learning Strategies Shape What, When and Whom to Copy Learning that is facilitated by observation of, or interaction with, another individual or its products, is known as '**social learning**' (see Glossary) [1, 2]. Social learning is common in animals [2], reaching its zenith in the uniquely powerful, cumulative and diverse culture of humanity (see [3]). Such social learning is undoubtedly partially reliant on the same, or similar, mechanisms as asocial learning (namely associative learning), although, we argue, social learning is not *solely reliant* on associative learning mechanisms (Box 1). While social learning (or copying) appears intuitively useful, over the last 30 years, researchers from several fields have increasingly come to recognize that it is not inherently adaptive. Certainly, animals (including humans) may gain fitness benefits by learning from others insofar as they acquire adaptive information while avoiding some of the costs associated with the acquisition of **asocial information** such as time/energy loss, opportunity costs and exposure to predation whilst engaging in trial-and-error learning. However, the use of **social information** does not guarantee success [4-7]. Theoretical models predict that social learning will not be employed in an indiscriminate manner [5, 8]. Instead, heuristics, or "**social learning strategies**" (SLSs) (also termed "transmission biases"), are expected to bias individuals to copy particular behaviours ("what" strategies), performed by specific others ("who" strategies), under suitable circumstances ("when" strategies) [5, 8].

The SLS concept does not require that individuals be consciously aware of following a strategy and implies nothing about the underlying neural mechanisms [8]. Understanding the extent to which such strategies are products of evolution and/or learning requires detailed experimentation [9, 10]. Nonetheless, selectivity in social learning may have important

consequences, including facilitating the cultural inheritance of information and helping to promote **cumulative culture** by ensuring accurate copying of traits with high utility (whether instrumentally – 'success bias', or conventionally – 'prestige bias') as well as incorporation of novel beneficial modifications ('payoff bias') [11-13] (see Figure 1).

Here, we evaluate the status of SLS research for a cognitive science audience, briefly summarizing theoretical predictions and empirical evidence, discussing challenges to the SLSs approach, and providing a perspective on future progress that emphasizes the need for interdisciplinary work integrating mechanism and function. Our objective is to update and tighten the concept of SLSs and, in the process, build bridges between the disciplines that study social learning, including cognitive psychology (e.g. [14]), comparative psychology (e.g. [15, 16]), developmental psychology (e.g. [17]), anthropology (e.g. [18]), archaeology (e.g. [19]), behavioural ecology (e.g. [20]), neuroscience (e.g. [21]) evolutionary biology (e.g. [22]) and behavioural economics (e.g. [23]).

Findings of Social Learning Strategy Research

There is now evidence for various SLSs that shape when, what and whom to copy (Figure 1). Thus far, most species studied appear to show evidence of multiple SLSs. However, more systematic research is required to identify any phylogenetic patterns in the adoption of specific SLSs. Here we give a non-exhaustive review.

Copy when asocial learning would be costly

Theoretical analyses conclude that, as the costs associated with acquiring accurate but expensive personal information increase, reliance upon less accurate but cheap social information should increase [5, 55]. Empirical support is provided by experimental studies of humans [9], bees [35], fishes [36] and monkeys [37], where individuals were found to be

more likely to use social information when the task difficulty (and thus the energetic or time costs of acquiring the task solution asocially) increased. For example, human subjects required to decide whether two pictures represented the same shape seen from different angles, or different shapes were more likely to choose to view social information on harder than easier trials, and after previously incurring high (versus low) costs of asocial information [9].

Copy when uncertain

Other theory predicts that individuals should use social information when they are uncertain, either because they possess no relevant prior information as their prior personal information is unreliable or outdated [5], or because, in relative terms, the accumulated knowledge of conspecifics is more reliable [4]. Empirical studies have supported these ideas. High-fidelity copying is observed amongst children that lack relevant personal information (e.g., [13]). Children even copy causally irrelevant actions when they are confronted with a difficult task and are uncertain how to solve it [30]. Adult humans reporting low confidence in task-related decisions [9] or unreliable personal knowledge [56] are most likely to use social information. Subsequent analyses establish that copying when uncertain is an adaptive strategy in enhancing task success [9].

In addition to humans, uncertainty due to a lack of personal information has a powerful effect on increasing reliance on social learning across multiple taxa, including fish [27], chimpanzees [28] and ants [29]. Moreover, the opposite is also the case; children are more likely to **innovate** and devise a novel method when the demonstrated method is unreliable in providing rewards than when they observe reliable demonstration [17].

Other state-based strategies

106 The decision to use social information is affected by other factors, including the age, social
107 rank, and reproductive state [57] of the learner. There is experimental evidence that children
108 choose to use social information more than adults [17, 41], perhaps because task-relevant
109 knowledge is accumulated during childhood. Similarly, infant and juvenile capuchin
110 monkeys pay more attention to others' foraging behavior than do adults [42], and likewise in
111 chimpanzees individuals are most sensitive to socially learning nut-cracking [43], and
112 humans or birds to learn speech or song [44] when juvenile. Low- and mid-ranking
113 chimpanzees are more likely to use social information than high-ranking individuals [28], a
114 pattern replicated in blue tits [45], and perhaps resulting from a tendency to attend to higher-
115 status individuals. Early-life stress (e.g. unpredictable food) can also shape social learning
116 strategies later in life [58, 59]. Finally, empirical tests with bats [32], and bumblebees [33]
117 indicate that individuals copy others when dissatisfied with the payoff of their current
118 behaviour [34].
119
120 ***Model-based biases or "who" strategies***
121 Another important insight of theoretical models is that social learning may be *indirectly*
122 biased. That is, individuals may copy any aspect (e.g., the haircut or diet choices) of an
123 individual who is, for example, of high status, whether or not that trait helped the model
124 attain high status [5]. There is considerable empirical evidence for model-based biases in
125 both humans and other animals. For example, children prefer to copy high-status individuals,
126 where status is evidenced by their older age, popularity and social dominance [47], and they
127 distinguish between unfamiliar adults, copying the most 'prestigious' (or most attended to)
128 amongst them [48]. Moreover, for the acquisition of skills children prefer to copy adults over
129 their same-age peers, even when the peer appears to have greater task-relevant knowledge
130 than the adult [12]. Adults also display prestige-bias. For example, Fijian villagers trust the

advice of a successful yam grower with regard to a different domain, use of medicinal plants [11].

In non-humans, capuchins preferentially attend to and learn from older and higher-ranking over younger/lower-ranking individuals [42], whilst chimpanzees preferentially observe and copy dominants [46, 28] as well as those with a history of proficiency in similar tasks [46, 49]. These strategies are heuristics thought to lead to the copying of successful individuals (e.g., in reaching older ages or higher dominance rank), who are assumed to display behavioural traits worth adopting.

Frequency-dependent biases or "copy the majority" strategies

A positive frequency-dependent bias (aka "conformist transmission", "copy-the-majority") occurs when the most common variant in a population is disproportionately more likely to be adopted, allowing individuals to benefit from others' collective wisdom. Whether and under what circumstances individuals are expected to display this bias has excited controversy amongst theoreticians [5, 52, 57], and the empirical evidence is somewhat equivocal [9, 52, 60]. A key, though hotly debated, question is whether the behaviour of the majority of individuals should be copied, not simply the behaviour seen most [62-64]. In agreement with the emphasis on individuals rather than behaviour, children and chimpanzees will copy the behavior demonstrated by three different individuals over the behavior demonstrated, three times, by one individual [65]. To some extent, the debate is alleviated by recognition that conformity is often just one of several simultaneous influences on behavior (see *Multiple strategies are deployed simultaneously* and Figure 1) and is sensitive to context. Children show higher-fidelity imitation when demonstrations involve two simultaneous models, rather than one model [66]. Likewise, children will copy with higher fidelity when provided with linguistic cues indicating there is a convention to be followed compared to when instrumental

156 language cues are provided [66, 67]. Other studies of humans suggest the likelihood of
157 conforming is context- [52] and individual-dependent [53], and sensitive to whether the
158 demonstrators have obtained their information from independent sources or from each other
159 [14].
160
161 ***Content-dependent biases or "what" strategies***
162 Content-dependent (aka "direct") strategies express biases regarding *what* is learned, with
163 individuals adopting behaviors following direct assessment of the (relative or perceived)
164 value of the trait. This assessment can be based on the nature of the information itself, or its
165 effectiveness. In the former case, humans express a preference for social (e.g. relationships)
166 over physical (e.g. the weather/environment) content when transmitting stories, urban
167 legends, or gossip [68, 24], and for content that evokes strong emotions (e.g., disgust), or of
168 survival relevance [24]. Such preferences are usually referred to as content biases. The payoff
169 associated with a trait is also known to affect transmission ('payoff bias' [e.g. 70]). There is
170 empirical evidence of preferences for more effective solutions (i.e. *copy a trait if its payoff is*
171 *better than your own*) across a range of species, including sticklebacks [69], and chimpanzees
172 [25, 70, 71].
173
174 **Novel Insights from Theoretical and Empirical Findings**
175 Several key insights have emerged over the recent years of intensive investigation of SLSs.
176 These include findings of considerable flexibility in the use of SLSs at both the individual
177 and population level, and of several SLSs being deployed simultaneously. Accordingly, it is
178 now understood that population-level patterns are not necessarily indicative of particular
179 SLSs. Finally as SLSs are imperfect heuristics, they can result in the acquisition and spread
180 of maladaptive behaviour.

181

182 ***Flexible strategy use***

183 Social learning strategies, and the behaviours that underpin them, are subject to natural
184 selection. This has led some researchers to characterize SLSs as implying inflexible decision
185 rules [72], but the fact that a strategy may have evolved does not imply anything about the
186 flexibility of the behaviour it generates (nor is flexible use of SLSs evidence that the SLS has
187 not evolved) [73]. Several recent studies have shown that individuals from the same
188 population can adopt different strategies depending on subtle differences in context [74],
189 developmental experience [59, 75], or other inter-individual variation [76, 77] accounting for
190 different patterns of behaviour. For instance, whom children copy (e.g. parents vs peers)
191 varies with task domain [74], with new skills learned preferentially from adults, but toy,
192 clothing and dietary preferences disproportionately learned from other children. Likewise,
193 children's learning strategies change as they age, with younger children influenced by
194 unanimity, but older children sensitive to majorities [78]. Moreover, there is increasing
195 evidence for cultural variation in reliance on social learning due to cultural differences in
196 experience during ontogeny, for example regarding care-giving practices [79], pedagogical
197 styles [80] or other emphases [81]. In humans, cumulative culture relies on psychological
198 adaptations that are "sufficiently flexible to support the acquisition of highly variable
199 behavioural repertoires" [82 pg 7877]. Together, these findings need not imply active or
200 executive control of decision-making, although that is a possibility. Hence SLSs are best
201 regarded as biases shaping behaviour, not hard-and-fast rules blindly applied across all
202 individuals or contexts.

203

204 ***Multiple strategies are deployed simultaneously***

There is now clear evidence for multiple strategies being deployed by the same species (e.g. humans, [83]; capuchins, [75]), often simultaneously (chimpanzees, [28]; sticklebacks, [36]; humans, [9]; Figure 1). For example, young children can combine different model-based biases (specifically "copy adults over peers" and "copy knowledgeable over ignorant individuals") contingent on whether the specific model characteristics intersect [12]. Learning biases can also interact flexibly to produce effective decision-making and higher payoffs in adults (e.g. individuals conform to the majority only when there is good consensus amongst demonstrators; [9], Figure 1). One study alone has provided evidence for the simultaneous deployment of nine strategies across a population of human adults [9], implying that SLSs likely operate in concert as biases rather than being combined into fine-grained decision rules [2] (although we note that most studies lack the resolution to distinguish between different individuals pursuing alternative strategies and individuals pursuing multiple strategies simultaneously). These findings undermine any research agenda dedicated to working out *the* strategy implemented by a particular species. Rather, the challenge is to determine the complex of strategic copying influences that shape behavior in any given instance.

Psychological heuristics and population-level patterns

In the SLS literature the term 'strategy' has often been used to describe both the psychological rule deployed by the learner and the pattern of behavior that this rule produces across the population. However, this has proven problematic, since studies have established that there is not necessarily a one-to-one correspondence between the two. For example, theory predicts that the conformist rule "copy the majority behavior" results in the disproportionate adoption of popular traits at the expense of rare traits, producing at the population level an S-shaped relationship between trait frequency and probability of adoption

[5]. However, conformist social learning does not result in the expected (S-shaped) population-level outcome when other, simultaneously operating, biases have a masking effect [9]. Humans are only seen to be conforming to the majority when the effects of other biases have been statistically removed [9]. This insight helps to explain conflicting findings over the extent of conformity.

Likewise, strategies such as "copy kin", "copy friends", "copy dominants", or where preferences differ between individuals (e.g. for dog breeds, or baby names), can result in population-level patterns that resemble random or "unbiased" copying (e.g. [84]) or, indeed, conformist transmission [63]. Given that multiple learning rules can generate the same population-level pattern, whilst a particular learning rule can generate multiple population-level outcomes, it is recommended that the term 'strategy' be restricted to cognitive rules and not population-level patterns of behavior [2].

Herding and the spread of misinformation

When the cost of collecting personal information and of individually vetting every trait for its potential contribution to fitness is prohibitive, individuals may rely on imperfect heuristics that enable them to adopt reasonably good behaviour through social learning now. As a consequence, some maladaptive behaviours will be acquired [85]. For example, reliance on social learning has resulted in the copying of obviously causally irrelevant behaviours in children (e.g., [17, 86, 87]) and potentially the recent spread of fake news, where content-dependent biases may play an important role [88]. Maladaptive information cascades [4], whereby individuals disregard their own personal information in favour of following the decisions of others (not the cues on which those decisions are based), may also occur. This may explain the explosive spread of behaviours such as economic market crashes, mob

violence, panic rushes in crowds and even suicides, as well as the existence of witchcraft and fake medical treatments [85, 89, 90].

Challenges to the Social Learning Strategy concept

The strong empirical support for strategic copying has not prevented the SLS concept from attracting criticism. Below we consider some major criticisms, which require a clarification and updating of the SLS concept.

Do SLSs imply domain-specific mechanisms?

Comparative psychologists have claimed that the SLS perspective encourages the conclusion that SLSs are reliant on 'specialised', 'evolved' or '**domain-specific**' mechanisms that deploy 'conscious', 'voluntary' decision-making [72, 91, 10, 16]. It has been claimed that such assumptions could be leading the field astray as such authors suggest that **domain-general** associative processes could also account for the findings of SLS experiments. *Prima facie*, this criticism would seem an attribution error, perhaps a consequence of differences between fields in their use of terms such as 'evolved' (which, as we deploy it, applies to exaptations and products of cultural evolution, not solely biological adaptations). The SLS literature has been explicit from the outset in disavowing any commitment to mechanism, or to conscious decision-making. The paper that introduced the SLS concept states [7 p5]:

> "*In accordance with behavioral ecologists' use of the phenotypic gambit (Grafen, 1984), it does not matter whether animals adopt such strategies as a consequence of evolved psychological mechanisms, learning, culture, or some combination of processes"* and *"the adoption of such strategies would not require that the animals be aware that they are following a strategy, nor that they understand why such strategies*

279 *may work."*

280

281 The subsequent SLS literature is replete with statements along these lines (e.g., [69,
282 92, 9, 93, 2, 77], highlighting SLSs researchers are not committed to the hypotheses that the
283 behavior is unlearned, under tight genetic control, nor that decision making is conscious.
284 Naturally, the neutrality of the SLS concept does not preclude experimental findings
285 suggesting the possibility of social learning adaptations. Recent research with children,
286 chimpanzees, and gorillas may provide evidence of evolved aspects of SLSs; individuals
287 showed enhanced learning from animate (compared to inanimate) models, which was not
288 merely due to changes in input mechanisms (e.g. reduced attention), but to greater depth of
289 encoding and enhanced memory with socially mediated events [94]. This may be due to an
290 'agentive match' between model and observer [94], implying some SLSs may be
291 manifestations of evolved enhancements in memory for, and thus replication of, the actions
292 of specific models, mediated by relatability of goal-directed actions between observer and
293 model (also see Box 1).

294 However, any claim that the evolutionary reasoning of SLS leads researchers to
295 expect that closely related species should exhibit similar strategies [72] is highly contentious.
296 While closely related species are generally expected to exhibit trait similarities, behavioural
297 traits are renowned for being evolutionarily labile. Experimental studies have shown different
298 SLS use in closely related species, different populations of the same species [95, 109], and
299 different individuals within a group [76, 77], whilst other studies imply that ecology may be
300 more influential in SLS distribution than phylogenetic relatedness [92, 110]. There is a need
301 for further research on the relationship between phylogenetic relatedness and SLS use, but
302 the prevailing evidence suggests that, due to the demonstrated flexibilities in employment of
303 SLSs, their study requires no commitment to the nativist stance that SLSs are unlearned.

Are SLSs an alternative to associative learning?

The misattribution of domain-specific explanations to SLS studies has led to **associative learning theory** (henceforth ALT) being juxtaposed as providing alternative domain-general explanations to SLSs [91, 10, 16, 72]. There is no question that the findings of social learning experiments can often be explained by associative learning, but SLS and ALT are not alternatives. SLSs provide a functional account of behaviour; they are explicitly mechanism-neutral, and no substitute for thorough analysis of mechanism. This is implicit in the literature, as SLS studies commonly deploy **asocial learning** controls, and consider ALT explanations for the results (e.g. [95, 32, 27]; see Box 2).

The possibility that ALT could underlie SLS findings does not, however, constitute evidence that alternative mechanistic explanations are wrong, as some researchers have implied [72, 91]. For instance, researchers have argued that between-species differences in social learning, such as differences between humans and chimpanzees in imitation, reflect differences in 'input mechanisms' (i.e. perceptual or motivational factors), on the assumption that both species exhibit the same ALT learning processes [91]. However, it would seem implausible, given the extensive evidence for neurological and genetic differences between these species (e.g. [108, 110]), to suggest motivational variation could fully explain the differences in social learning between chimpanzees and humans. Equally, the possibility that humans learn through the same mechanism(s) as nonhumans, but with enhanced computational power resulting in faster operation and differing behavioural effects, merits attention [108].

Is "blackboxing" of mechanism bad?

SLS research has relied heavily on an assumption known as the "**behavioural gambit**", the idea that mechanisms of implementation do not greatly constrain the adaptive behavioural rules that evolve [20]. This assumption has stimulated extensive theoretical work, which in turn allows SLS theory (e.g. [112, 113, 6, 34]) to guide a great deal of empirical research [110, 93, 70]. However, other researchers have expressed concern that this 'blackboxing' of mechanism is 'no longer a tenable scientific strategy' [15, p2]. Is this the case, or have the perils been overstated?

The critique focuses on the findings of a computer-based tournament that pitted learning strategies against each other in an evolutionary simulation [114]. The tournament revealed how individuals performing the highest-payoff behaviour in their repertoire inadvertently filter information for others to copy. Thus, social learning will be favoured in any exploration/exploitation dilemma, if there is an opportunity cost to exploration (asocial learning) and individuals can select the best behaviour known to them for exploitation. This general adaptiveness of social learning is an important explanation for the ubiquity of social learning in the animal kingdom [114].

The conclusion that social learning is adaptive across a broad range of conditions, a robust finding of experimental studies and formal theory [2, 5, 83, 93, 115], has nonetheless been described as 'misleading'. Critics argue that some asocial learning in the tournament (where individuals asocially obtained information about the payoff of a behaviour they had already learned by performing it) was not properly accounted for in the analysis and interpretation of the tournament results, effectively obscuring (or,'blackboxing') an important source of asocial information, and leading to an unwarranted emphasis on social learning [15]. However, this argument is problematic, in two respects. First, it does not distinguish between two classes of learning represented in the tournament – learning how to perform a behaviour and learning its payoff – when the claims regarding the superiority of social

353 learning were related explicitly, and specifically, to the former. Unravelling how individuals
354 decide which of a virtually infinite set of behaviours to learn is a serious scientific challenge,
355 in comparison to which updating payoffs received for established behaviour appears
356 straightforward. Second, and more importantly, disagreement over how to interpret learning
357 about payoffs reflects little on the perils or merits of 'blackboxing'. The tournament
358 organizers decided that details of exactly how learning about payoffs happened were
359 peripheral to the analysis, and so these were abstracted out. Theoretical models must always
360 strike a balance between accurately representing the process being studied and incorporating
361 those assumptions that are judged critical, while deciding which details to leave out. In this
362 respect, the critique of 'blackboxing' applies to any mathematical model. It is, of course,
363 quite legitimate to evaluate any model on the extent to which it has accurately captured the
364 key components of the process being studied. Nevertheless, it is a big step indeed to build on
365 such critiques a proposal that the entire approach of not modelling every mechanism in detail
366 is scientifically 'untenable'.

367 Whilst systematically and uncritically ignoring mechanism would indeed be
368 problematic, evolutionary researchers are not unaware of these pitfalls – indeed there is
369 active debate within the field about the issue (e.g. [20]). There is no doubt that research on
370 the neural mechanisms of social learning is important, but we note that such research itself
371 attests to the underlying biological reality of SLS, as well as neural adaptations for social
372 learning competences (particularly in humans). Some of the very latest neuroscience research
373 is revealing just how profoundly social interactions are embedded in human and nonhuman
374 brains. For example, there is growing, and methodologically diverse, evidence indicating that
375 a brain region known as the ACCg (the anterior cingulate cortex lying in the gyrus) is
376 specialised for the processing of social information in humans and nonhumans, with
377 ramifications specifically for SLSs (see Box 3). Likewise, 'evolutionary neuroscience'

experiments indicate that differences between primate species (including humans) in neural connectivity and responsivity of the mirror system link to species differences in the capacity for imitation and social learning of tool use [121]. In macaques and chimpanzees, most of this circuitry consists of frontal–temporal connections, whilst humans have more substantial temporal–parietal and frontal–parietal connections. Moreover, humans' comparatively expanded and plastic association cortex [122] may imply a greater role for developmental scaffolding [123] upon brain architecture underlying social learning capacities in humans versus nonhumans (but see [124]). Finally, connectome studies are revealing dedicated networks of neural connections underlying behavioral innovation [125], that link to regions of the primate brain (such as the lateral prefrontal cortex) that have expanded disproportionately during human evolution [126]. Such neuroscientific studies highlight how functional and mechanistic perspectives are complementary. Moreover, they leave the hypothesis that social learning abilities underlying SLSs derive solely from selection on input mechanisms (e.g. attention or motivation) [91] increasingly untenable.

Metacognitive SLSs

It has been suggested [16] that the primary difference between cultural evolution in humans and other animals is that humans alone possess domain-specific **metacognitive** SLSs, whereby individuals consciously assess who is knowledgeable, which in turn influences whom is copied (see Box 4). In reality, the discrepancies between humans and other animals in this domain are multifaceted, and almost certainly reflect the aforementioned substantial evolved differences in the neural architecture of human brains [108], rather than a single cognitive competence. Nonetheless, an important role for metacognition in human culture is highly plausible. One possibility is that human-unique metacognitive SLSs produce reportable representations of 'who knows', thereby supporting the cultural inheritance of

403 'wise' SLSs dictating high-fidelity copying from recognized experts (and avoiding copying
404 amateurs), which over generations promotes cumulative cultural evolution [16]. Importantly,
405 for arguments that emphasize the importance of culture for the ecological dominance of
406 humanity [135-137], these metacognitive strategies enable individuals to copy the best trait in
407 a given domain, despite the reason for its success being cognitively opaque. By allowing
408 inferences to be made about the goals and intentions of others, a metacognitive capability
409 potentially affords more accurate reconstruction of the nature of the task to be copied, whilst
410 the same capabilities potentially help tutors tailor their teaching and scaffolding to pupils'
411 knowledge levels. Although SLSs have thus far been constrained to the perspective of the
412 learner, it might be fruitful to explore how SLSs may be extended to include strategic
413 information provisioning by experts.

414 While the 'metacognition underlies human culture' argument was presented as an
415 alternative to a SLS explanation [16], this juxtaposition is misleading, both because to our
416 knowledge, no strong claims about SLSs underlying human-animal differences appear in the
417 literature, and because metacognition itself may be a mechanism underpinning some SLSs.
418 The SLS concept covers a diversity of mechanisms for achieving efficient social learning,
419 from genetically heritable variation between individuals through to the social learning of
420 social learning [75] and the cultural diversity the latter entails [81, 136]. Given that the
421 phylogenetic distribution of metacognition is an active area of research [138], it would seem
422 premature simply to assume that "*all* animal behaviour … conforming to SLSs, is based on
423 domain-general processes of associative learning" ([16, p209] emphasis added; see Box 1).
424 Nonetheless, increased attention to the role of metacognition in social learning and teaching,
425 in humans and other animals, is required (see Box 4). The hypothesis that metacognitive
426 SLSs are uniquely human merits further attention.
427

Concluding Remarks

The SLS perspective has proven productive not least because the approach provides a vehicle for integrating cognitive, behavioural and evolutionary perspectives, as well as empirical work and theory. A complete understanding of behaviour requires that (at least) **four questions** are addressed [139]. Analyses of social learning and cultural evolution that focus on function to the exclusion of mechanism are necessarily incomplete. However, SLS researchers have conducted numerous investigations of social learning mechanisms, including drawing on associative learning interpretations (e.g. [107, 140, 141]). To move forward, what is now required are not retrospective narrative accounts but experimental tests, based upon *a priori* specification of differing predictions, designed to distinguish purported alternative explanations of social learning behaviour (see *Outstanding Questions*). There are exciting opportunities for integrating functional, evolutionary, developmental and mechanistic analyses in this domain, for example, by exploring the mechanistic and neuroscientific bases of strategy use (Box 3), studying how learning strategies change over developmental time as cognitive capabilities change, investigating the phylogenetic distribution and adaptive value of the use of a particular SLS, and exploring the role of metacognition in human culture (Box 4). The advantages of interdisciplinary work in these domains extend beyond the benefits that return to social learning researchers. For instance, it may be possible for developmental psychologists, comparative psychologists and cognitive neuroscientists to make sense of population or individual differences in cognitive development or neural connectivity in terms of alternative SLS deployment. Likewise, species differences in brain architecture, and its development throughout ontogeny, will likely be strongly tied to the details of the functional questions those brains have evolved to answer. In comparison to the cruder categories of ‘social learning’ or ‘imitation’, specification of SLSs characterizes, for instance, whether the learner will be attending to

453 payoff, consensus, or status information, each of which are seemingly associated with
454 distinctive patterns of neural connectivity (Box 3). Given their impressive track record of
455 integrating empirical and theoretical insights, as well as findings from behavioural and
456 evolutionary biology, cognitive neuroscience, and developmental psychology, SLSs
457 potentially provide a useful vehicle for bridge-building between fields.

458

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464

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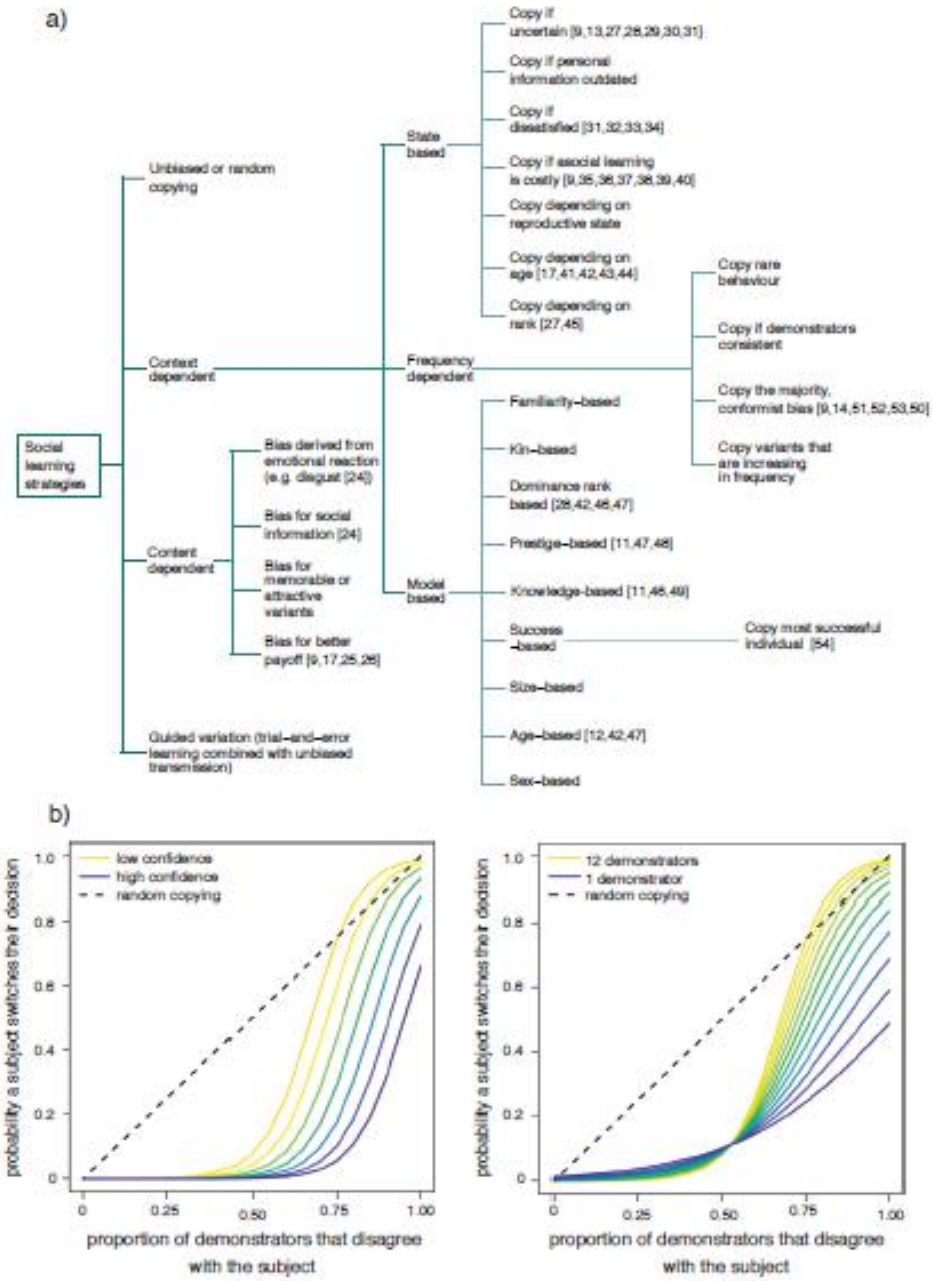
Figure 1. Summarising identified social learning strategies and their use (a) Social learning strategies for which there is significant theoretical or empirical support (based on Figure 1 in [93]). The tree structure is purely conceptual and does not imply similarity of cognition. Sources are purely for illustration as recent literature entry points for readers (see [93] for additional illustrative sources). (b) The panels, which derive from an experimental study of human social learning [9], illustrate how behavioural outputs can result from the simultaneous deployment of multiple social learning strategies. The left panel shows how subjects' decisions were affected by both their personal confidence and consensus amongst demonstrators, whilst the right panel shows the combined effects of the number of demonstrators and the consensus among them. Based on Figure 2a (left) and 2b (right) in [9].



BOX 1: Mechanisms of asocial and social learning

Some authors have proposed that associative learning mechanisms can explain *all* social learning, and even suggested that the term 'social learning' is misleading because the underlying mechanisms are not distinctively social [91, 10]. Attributing social learning only to associative learning mechanisms, however, relies on a narrower definition of social learning than standard [1, 2], excluding language and teaching which are reliant on specialist mechanisms. Here we review key evidence regarding the debate.

Social learning in 'asocial' species has been interpreted as evidence that social learning relies on *only* asocial mechanisms [91, 10]. However, social learning from heterospecifics is well-established [95, 96], and all animals, even solitary, are exposed to social information (observation/products), from mates, broodmates, or territorial neighbours [97]. Hence, it is dubious to infer that solitary species should not experience selection for social learning, or that their social learning relies on asocial mechanisms only. We may, however, ask how evolutionary histories of group-living shape social learning's evolution [97]. Currently, it is not known whether social species exhibit evolved enhancements in social learning.

Social and asocial learning abilities co-vary across primates [98], but this does not negate the possibility of separate capacities that have coevolved. The correlation is imperfect, leaving variation potentially explainable by evolved adaptive specialization in social learning, as seen in vocal learning in songbirds, cetaceans and humans [99], public-information use in sticklebacks [95], and teaching in humans and other animals ([97] See Box 4). Experimental studies are equivocal, with some reporting a positive (humans: [101]; birds: [45]), and others a negative (sparrows: [102]; marmosets: [103]), relationship between asocial and social learning performance.

836 **Bumblebee research** is enlightening here. It has been hypothesised that social
837 learning is second-order conditioning whereby bees associate conspecific presence with
838 reward and then associate conspecifics with a rewarding flower colour [104]. However,
839 bumblebees learn differently when trained with social versus inanimate cues [105], and rely
840 on social, over asocial, learning when tasks are complex [35] or the environment variable
841 [106]. These experiments and 'ghost controls' in several other species [107] indicate animals
842 respond differently to social and asocial information, again implying that enhancements in
843 social learning performance can evolve.

844 Although there is undoubtedly overlap between social and asocial learning, whether
845 (language and teaching aside) they rely entirely on the same mechanisms remains unknown.
846 Indeed, for many social species learning occurs more frequently in social than asocial
847 contexts. These species may have experienced selection for proficient social learning, with
848 enhanced asocial learning likely a by-product (e.g. humans [108].)

849

850

851 **BOX 2: Storytelling and Science: Contention over SLS experimental investigations**
852
853

854 Criticisms of SLS experiments by learning theorists [72] have sparked debate. Here, we
855 present three illustrative studies, then draw out general points.

856

857 **1. Foraging frog-eating bats learn novel prey cues socially** more readily when cues are
858 rewarded only 50% of the time compared to 100% of the time (a 'copy-if-dissatisfied' or
859 'copy-when-asocial-information-is-unreliable' SLS) [32]. Learning theorists suggested that
860 social learning in the 50%-rewarded treatment may have been an artefact of bats being more
861 likely to visit the demonstrated cue source than in the 100%-rewarded treatment because

862 intermittently-rewarded stimuli are less attractive [72]. However, the findings of an asocial
863 control treatment rule out this explanation.
864
865 **2. A species difference in public-information use**. Three- and ninespine sticklebacks
866 experienced two groups of fish feeding at different rates (rich and poor prey patches). Later,
867 when tested in the absence of demonstrators, only ninespines showed a preference for the rich
868 patch, perhaps because ninespines face greater predation risk than threespines (a 'copy-when-
869 collecting-asocial-information-is-costly' SLS) [95]. Learning theorists suggested this finding
870 is an artefact of fish detecting that more prey were delivered at the rich patch [72]. This
871 explanation is not credible because (i) the design explicitly prevented observers from seeing
872 food, (ii) fish cannot locate the rich patch using odour cues alone [95], and (iii) later studies
873 using watertight chambers to house demonstrators and feeders separately obtain identical
874 results [111]. Moreover, the associative learning (ALT) account cannot explain the between-
875 species differences in public-information use under identical conditions.
876
877 **3. Minnows were more likely to use social information when predation risk was high** (a
878 'copy-when-asocial-learning-is-costly' SLS) [39]. Learning theorists proposed that predation
879 risk caused conditioned suppression of the feeder-food association, reducing foraging
880 motivation, leading fish to approach areas where conspecifics had been [72]. This is
881 extremely unlikely as fish perceiving risks are more likely to remain in cover than join shoals
882 in the open (see [39]).
883
884 ALT is a powerful explanatory tool, which can be fruitfully deployed to understand
885 findings from social learning experiments. However, these examples illustrate how the utility
886 of ALT does not guarantee that a particular ALT explanation is correct. The general point

here is that mechanistic perspectives that ignore functional insights are no less prone to error than functional perspectives that ignore mechanism. To move the field forward, rather than retrospective ALT storytelling, researchers must integrate perspectives and experimentally compare the relative merits of alternative mechanistic explanations for particular exhibited strategies.

BOX 3: The Neurobiology of Strategic Copying

Social neuroscientists now recognize 'deep homology' in the mechanisms and structures of the 'social brain' across diverse taxa [115], whilst primatologists emphasize how the brain of primates, particularly with respect to encephalization and the neural basis of imitation, is organized for 'socio-cultural' processing [116]. That social interactions are embedded in brains is also highlighted by the emerging field of 'network neuroscience', which argues that neural networks within the brain exhibit reciprocal interaction with social networks in the environment: neural activities shape patterns of learning and behaviour in people's social networks, which in turn feed back to influence individuals' brain structure and function [117]. Human brains spontaneously encode social network positions of familiar others, highlighting how navigating complex social interactions could influence brain development and evolution [118] and hinting at rapid unconscious (see Box 4) processes underlying model-based SLSs in humans and nonhumans. Collectively, these findings imply that the use of particular social learning strategies within a population may lead to characteristic patterns of neural connectivity within individual brains, potentially with signatures of implemented strategies manifest across diverse animal groups.

Increasingly, neuroscientific data are pointing to dedicated mechanisms for social learning. For instance, Hill et al. [119] discovered that the portion of the anterior cingulate

913 cortex lying in the gyrus (ACCg) of humans showed neuronal activity corresponding to
914 reinforcement (or trial-and-error) learning, but only when monitoring the behaviour of others.
915 This allocentric pattern is distinct from other regions, implying it signals information crucial
916 to social learning [21]. Neurophysiology, neuroimaging, lesion studies and those of
917 individuals with autistic spectrum disorder, all indicate a specialisation in the ACCg for
918 processing social information in humans and nonhumans [120]. Other medial prefrontal
919 cortex (mPFC) subregions mostly signal in an egocentric frame or in both egocentric and
920 allocentric frames. Thus these regions may contribute to integrating information regarding
921 one's own actions and those of others to update behaviour [21], potentially underlying *copy if*
922 *better* SLSs. Likewise, considering frequency-dependent SLSs, there is evidence that the
923 magnitude of activity in the anterior insula, rostral cingulate zone, and ventral striatum in
924 response to consensus/non-consensus between demonstrators or between self and
925 demonstrators predicts changes in an individual's behaviour (see [58] for a review). It
926 remains to be established to what extent different people, societies and species implement the
927 same behavioural strategies in different ways in their brains, but this issue affords rich
928 opportunities for comparative work.
929
930
931 **BOX 4: Metacognition and Social Learning Strategies**
932
933
934 Metacognition is a sophisticated cognitive capacity developing late in human ontogeny [127],
935 considered uniquely human by some [16]. It uses forms of learning (e.g. ALT) and/or other
936 aspects of cognition (e.g. memory, mental simulation) to generate responses not directly
937 related to them (i.e. thinking about thinking). Metacognition is thus sometimes labelled a
938 *system 2* process, being top-down (executively controlled), available to conscious awareness,

939 in contrast to and serving to augment *system 1* activities which are bottom-up (stimulus
940 driven), involuntary and based on information from genetic inheritance or associative
941 learning (dual-process theory [128]). For example, humans may express their confidence (a
942 metacognitive output) regarding their own abilities, verbally or physically (e.g. shrugging
943 shoulders), or possess knowledge about what others know.

944 The extent to which metacognitive capacities are seen in nonhumans is relevant to our
945 understanding of their levels of self-awareness and evolution of the human mind. Although
946 nonhuman abilities may be less varied and sophisticated (e.g. [129]) than humans', there is
947 evidence in pigeons, rats, monkeys and apes for monitoring of knowledge, uncertainty and
948 memory, as well as confidence levels (reviewed in [130]). For example, chimpanzees make
949 spontaneous confidence judgements regarding the likelihood that they performed accurately
950 enough in a task to gain a reward, and adjust their behaviour accordingly [130]. Likewise,
951 strategic information seeking in nonhumans, where ALT explanations are discounted [131],
952 reflects a response to perceived uncertainty. For example, orangutans and chimpanzees
953 demonstrate that they *know when they don't know* which of three tools is appropriate to reach
954 a reward (due to their length being occluded) by changing position to determine this [132].

955 Whether explicit metacognitive capacities are manifest in SLSs, such that the
956 accuracy and reliability of cognitive processes in the self and others is *consciously* assessed
957 [16], is open to question. The majority of contexts where 'copy when uncertain' SLSs have
958 been reported need not require explicit (versus implicit) metacognition, but other strategies
959 representing 'who knows' (e.g. chimpanzees: [49]; humans: [133, 134]) might. While no
960 more an alternative to SLS than ALT, metacognition potentially affords unique learning
961 strategies (especially if explicit). These include enabling accurate inference of others'
962 intentions and hence what to copy, and teaching that is contingent upon, or enhanced by,
963 knowledge of the pupil's level of understanding. Thus, metacognition may have played an

important role in human cognitive and cultural evolution, and may help to explain how humans teach across such a broad range of tasks, in contrast to the rare and specialist teaching reported in other animals [108, 100]. However, whether explicitly (conscious) metacognitive SLSs are unique to humans and must produce reportable (verbally or otherwise) representations of 'who knows' to promote culture [16], is currently difficult to assess.

HIGHLIGHTS

- Accumulating evidence supports theoretical predictions that humans and nonhumans are selective in what, when and whom they copy, suggesting the use of "social learning strategies" (SLSs).
- Recent studies indicate that SLS use is flexible and changes with ontogeny, experience, state, and context.
- Multiple SLSs may be adopted simultaneously in the same population, and even by the same individual. Individuals' SLSs do not necessarily correspond to apparent population-level patterns.
- SLSs likely involve associative learning processes and social learning mechanisms; experimental controls indicate that associative learning alone cannot explain all SLS findings.
- Recent neuroscientific data suggest the anterior cingulate cortex in the gyrus (ACCg) may be specialised for processing the social information of relevance to SLSs.
- The role of metacognition in SLSs requires investigation.

OUTSTANDING QUESTIONS

- **What mechanisms underpin SLSs?** Investigating the behavioral and neurobiological underpinnings of SLSs is central to progress in the field. Can we design studies with differing *a priori* predictions regarding learning mechanisms involved in SLSs? Feasibly, the types of tests (including ALT controls, Box 2) deployed with bumblebees (Box 1) could be extended to other systems.
- **Do particular SLSs involve characteristic neural circuitries?** Do individuals, societies or species implement behavioural strategies in similar ways in their brains? Is there a characteristic connectome for each SLS? Can neurobiological studies (Box 3) shed light on the role of ALT in SLSs implemented by different species? How is SLS use influenced by individual differences?
- **How do SLSs develop over the lifetime?** The ontogeny of SLSs is understudied yet contributes to flexibility in SLS-use. How does the deployment of SLSs shift over ontogeny? To what extent is this contingent on general aspects of brain and cognitive development? How do individuals alter use of SLSs with personal experience and changing context (e.g. stage of tradition formation)?
- **What is the evolutionary history of SLSs?** Can phylogenetic techniques (e.g. comparative studies of SLSs in multiple pairs of closely related species) contribute to the debate over the extent to which SLSs are evolved adaptations and/or learned heuristics? Do differing evolutionary histories of group-living influence the use or sophistication of SLSs?
- **What is the adaptive value of SLSs?** SLSs likely vary in their fitness consequences but this is understudied and relies on identifying SLSs in natural contexts. How do SLSs affect foraging success and success in other domains (e.g. nest-building and predator evasion)?
- **What role does metacognition play in human culture?** What is the phylogenetic distribution of metacognitive SLSs (Box 4)? How do they promote culture? Is knowledge of 'who knows (what)' critical for model-based SLSs and teaching?

GLOSSARY

Adaptive strategy: a strategy that enhances survival and reproductive success of the individual adopting it.

Asocial learning (or **Individual learning**): learning for oneself through experience and/or trial and error.

Asocial Information (or **Personal information**): information acquired by an individual through their own activities and interactions with the environment.

Associative Learning Theory (ALT): the process whereby individuals learn an association between two stimuli (Classical or Pavlovian conditioning), or a behaviour and a stimulus (Instrumental or Operant conditioning).

Behavioural Gambit: the assumption that genetic architecture does not constrain the evolution of behavioural phenotypes. An extension of the phenotypic gambit to the evolution of behaviour [19, 115].

Copying: synonym for **social learning**

Cumulative Culture: a form of cultural evolution where individuals build upon the knowledge of previous generations such that trait complexity, diversity or efficiency increases across generations. Arguably unique to humans [116].

Domain-General Processes: psychological mechanisms thought to have evolved not to function in specific contexts but to be domain and taxonomically general. An example is **associative learning**.

Domain-Specific Processes: processes supported by specialised, and evolutionarily specified, psychological mechanisms. Being evolved to solve problems in a particular domain, sometimes perform poorly in other domains. Contrast with **domain-general processes.**

Four Questions: these define the complementary levels of analysis of behaviour proposed by Niko Tinbergen in 1963 (see [84]). They are often divided into two *how* questions: (1) How does it work? (mechanism) and (2) How did it develop? (ontogeny), and two *why* questions: (3) What is it for? (function or adaptation) and (4) How did it evolve? (phylogeny).

Innovation: we adhere to existing definitions in recent literature [117, 118]: *a new, useful, learned behaviour that may be transmitted to others, arising from asocial learning alone or in combination with social learning, that is produced to successfully solve a novel problem or an existing problem in a novel manner*. Novelty is often considered to be at the population level.

Metacognition: processes used to plan, monitor and evaluate one's knowledge and performance (e.g., thinking about thinking), or the knowledge/performance of others. In the context of SLSs metacognition refers to *knowing who knows* and *knowing what is known.*

Social Information: information acquired by an individual through some form of social influence (including social learning).

Social Learning: "learning that is facilitated by observation of, or interaction with, another individual (or its products)" [1, p207].

Social Learning Strategies: flexible rules that specify or bias when or how individuals should use social information, under various circumstances, to meet functional goals [7]. The term 'transmission biases' has, similarly, been used [5] to detail *when*, *what*, and from *whom* individuals acquire social information (see [77, 72]).